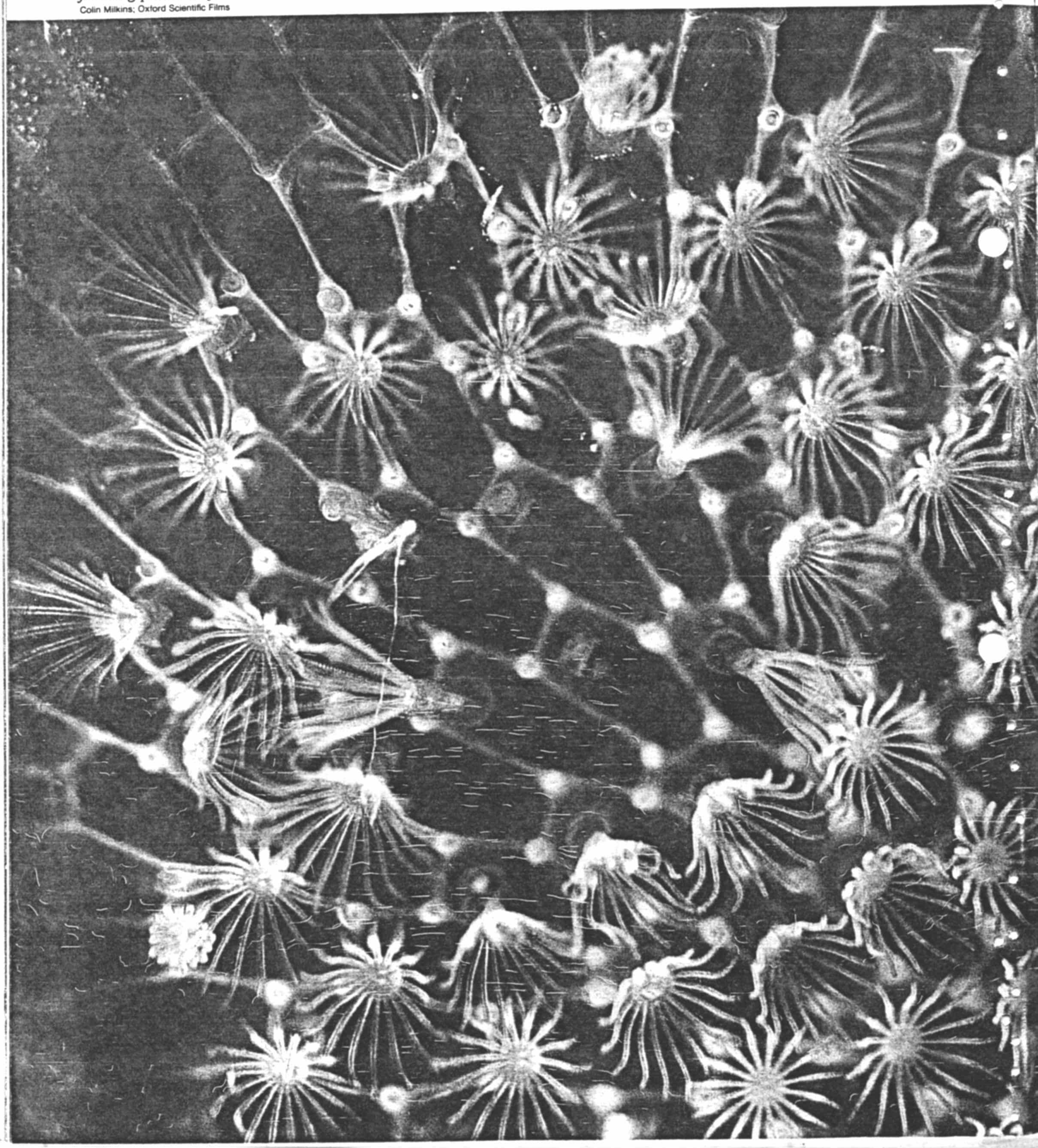
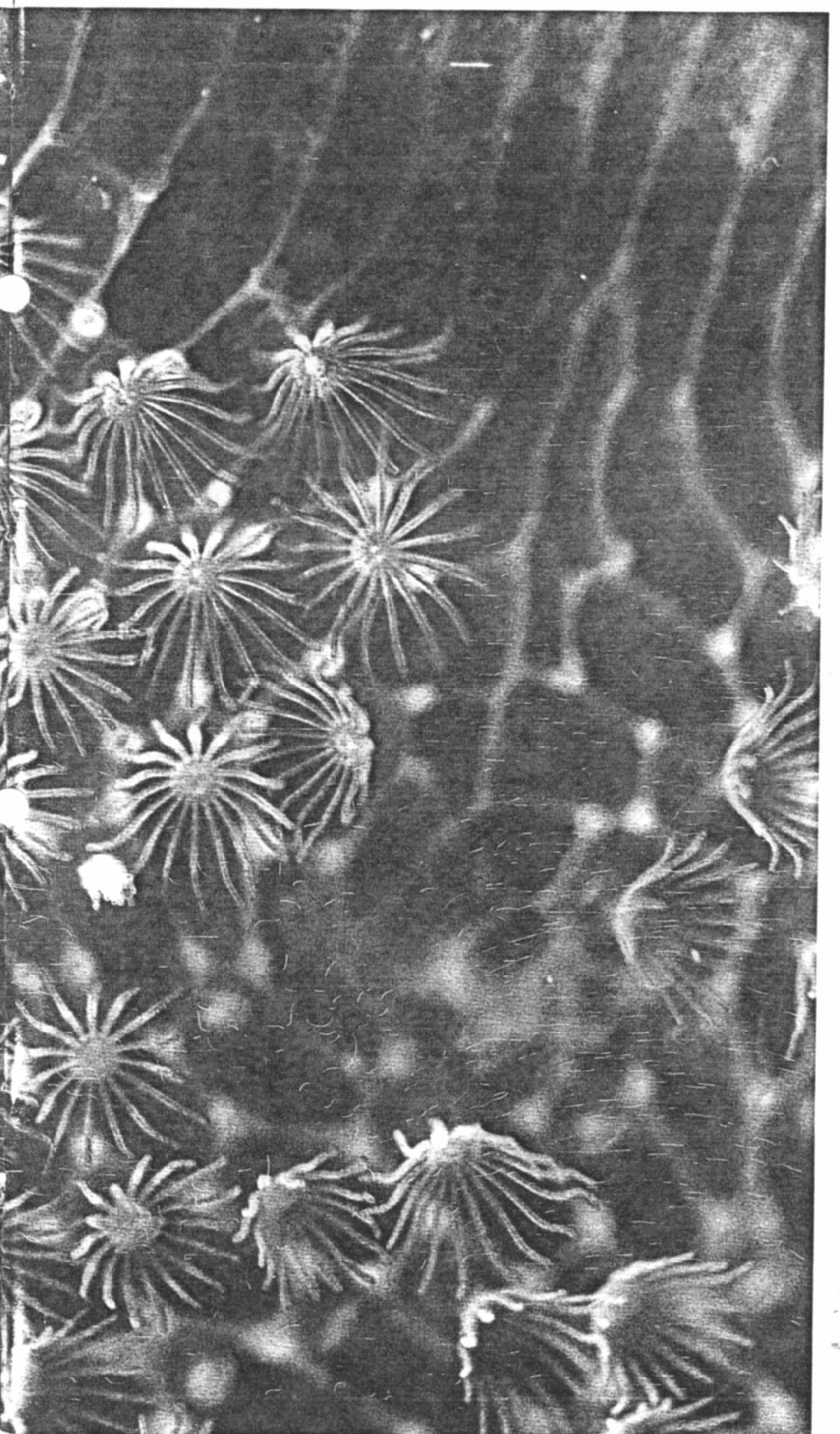
Most of its lophophores extended and waving, a colony of Membranipora membranacea*—also known as common sea mat or lacy crust bryozoan—feeds by filtering plankton from the water.*

Colin Milkins; Oxford Scientific Films



Turbulent World of Moss Animals

Common but little known, bryozoans can be found from the sea's edge to the abyssal depths



by Christopher G. Reed

Imagine that you are standing in an orchard in winter, the leafless branches of its trees forming a canopy overhead. The branches are in constant motion, buffeted by an unseen, turbulent wind that is drawn downward through the limbs and swirls over the ground around you. Now imagine that the wind is generated by the branches themselves, and that birds and insects are being sucked into a vortex above each tree and into a central gullet, where they are devoured. If you change the medium from air to water, you are visualizing a bryozoan colony. Except that the "orchard" is measured in inches, rather than acres, the "trees" are only one-fiftieth of a inch tall, and the living things being eaten are microscopic algae, bacteria, and flagellates. Bryozoans are among the most common invertebrates in the marine environment. But most people are unaware that the animals exist. The problem is that while bryozoan colonies are easy to see on rocks and algae, the individual members of the colony are microscopic.

Bryozoan colonies range from mossy feltworks to bushy arborescences to calcified incrustations to elevated, curled, leaflike growths that have the appearance and consistency of a handful of potato chips. They were first correctly identified as animals by an eighteenth-century French medical student, Jules Peysonnel, who was studying marine biology off the Ivory Coast. Peysonnel wanted to present his discovery to the French Academy of Sciences, but he wasn't allowed to address the academy because he wasn't a member. Instead, he asked a friend who was a member, René-Antoine Ferchault de Réaumur, to present the novel findings at the next meeting. Upon reading Peysonnel's paper, however, Réaumur decided its view deviated too radically from that expressed by Linnaeus and suppressed it to protect the reputation of his young friend. As a result, Peysonnel's account was never published, and he never received the proper recognition for his discovery, which was outlined in detail two decades later by an Englishman named John Ellis.

The stationary colonies of bryozoans

are composed of thousands of minute individuals called zooids, which, in incrusting forms, look like so many tiny marble coffins lined up next to one another. Each zooid consists of a calcified box, or zooecium, containing a digestive tract and a feeding organ. The feeding organ, a circle of ciliated tentacles, can be extruded from the zooecium into the seawater above the colony. This circle of tentacles is called the lophophore—the tree in the orchard analogy—and the tentacles, covered with thousands of cilia, are the branches. Coordinated beating of the cilia produces the currents that draw food into the center of the tentacular ring. Because of the geometric growth pattern of the zooids, the lophophores are regularly spaced throughout the colony; this spacing is what makes the colony more of an orchard than a forest. At the base of the cone formed by the tentacles is the mouth, equipped with a muscular pharynx that dilates reflexively, sucking in planktonic plants and animals that have collected in the vortex created by the feeding current.

Some species swallow and crush the food organisms in a gizzard before passing them on to the stomach to be digested. The digestive tract is recurved, ending in an anus that opens just outside the lophophore. The digestive tract and the lophophore are known as the polypide of the zooid; it can be retracted in microseconds into the protection of the zooecium by a pair of retractor muscles. Now imagine that the orchard around you can disappear in less than a second, each tree drawn into a chamber in the ground, leaving only a field of stubble and an abrupt quiescence, as in the eye of a hurricane.

I learned about the retractor muscles of bryozoans as a graduate student at the University of Washington. I was searching for a dissertation topic and was considering examining the ultrastructure of the lophophore of a local bryozoan. One night at the Friday Harbor Laboratories, I set about to snip off the extended lophophores to prepare for electron microscopy. I had a fine pair of iridectomy scissors, but not a very steady hand. Every time I tried to sneak up on an extended lophophore, the polypide would retract just as I snipped, and I would end up with just the ends of the tentacles. Finally, I quit in frustration and retired to the library to console myself. There, in the most recent issue of *Science,* was an article describing the lophophore as having the fastest-known contracting muscles. Reinforced by this evidence, I took the journal to my adviser's laboratory to show him that there was a reason for my failure. As I entered, my adviser, Richard Cloney, was bent over his dissecting microscope, enveloped in a haze of cigar smoke. "I have something to show you," I announced.

"Just a minute—look at this."

I bent over the microscope. In a little dish he had cut off ten to fifteen lophophores from the same species I was working on. "Now," he leaned back in his chair and puffed majestically, "what did you want?"

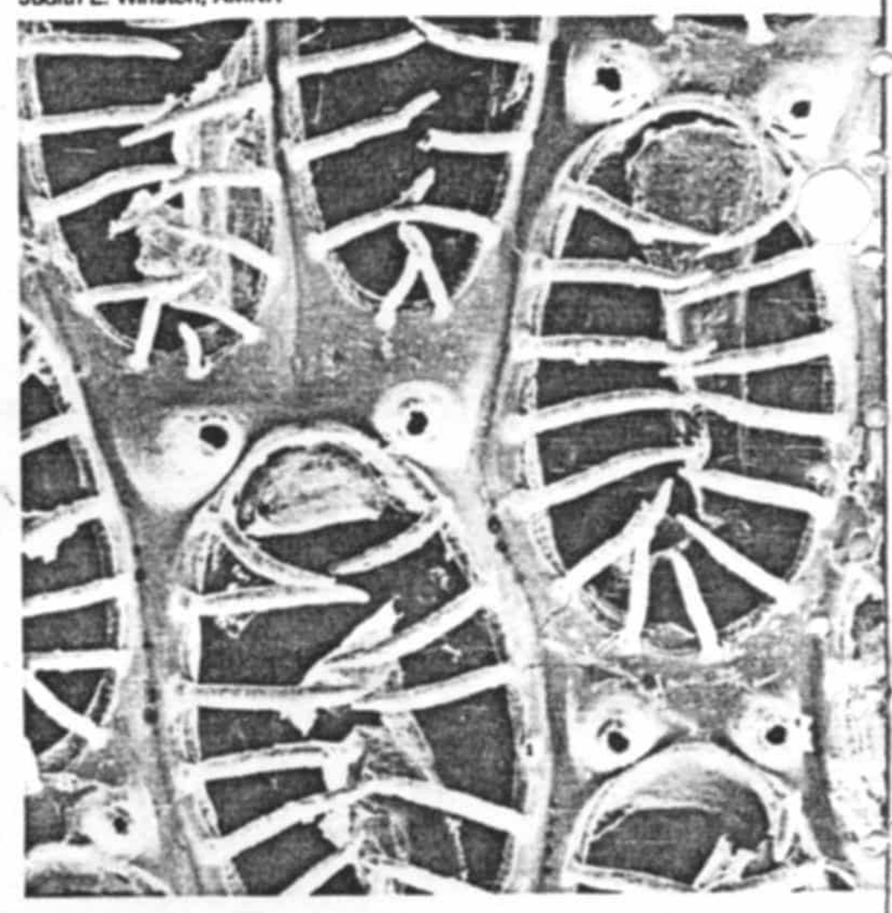
"Oh, nothing," I said, cramming the journal into my back pocket. In retrospect, I think I can explain his success without impugning my competence. The only rational explanation must be that the nicotine from the pall of smoke in his lab narcotized the animals.

Comparing an orchard with a colony of bryozoans is not as far-fetched as it may seem. Bryozoans share many characteristics of plants, probably because both plants and sessile animals are unable to move their base of attachment and therefore have evolved similar defense mechanisms. Some trees—poplars and sugar maples, for instance—produce more tannin in their leaves in response to increased attacks by herbivores. This regulated chemical defense makes the plants less digestible to such insect grazers as the gypsy moth caterpillar.

Like clusters of sugar maples or orchards, bryozoan colonies are vulnerable to predators. In this case, the predation is partial, since the entire colony is seldom killed. The main enemies of bryozoans are sea slugs, or nudibranchs; these big, lumbering, tanklike organisms crawl over the bryozoans, sliming their surfaces and seeking their weak point. The Achilles' heel of most bryozoans is their frontal membrane, which the sea slug gnaws through by rasping at it with a sliding belt

Kathleen B. Sarg; AMNH

Judith E. Winston; AMNH

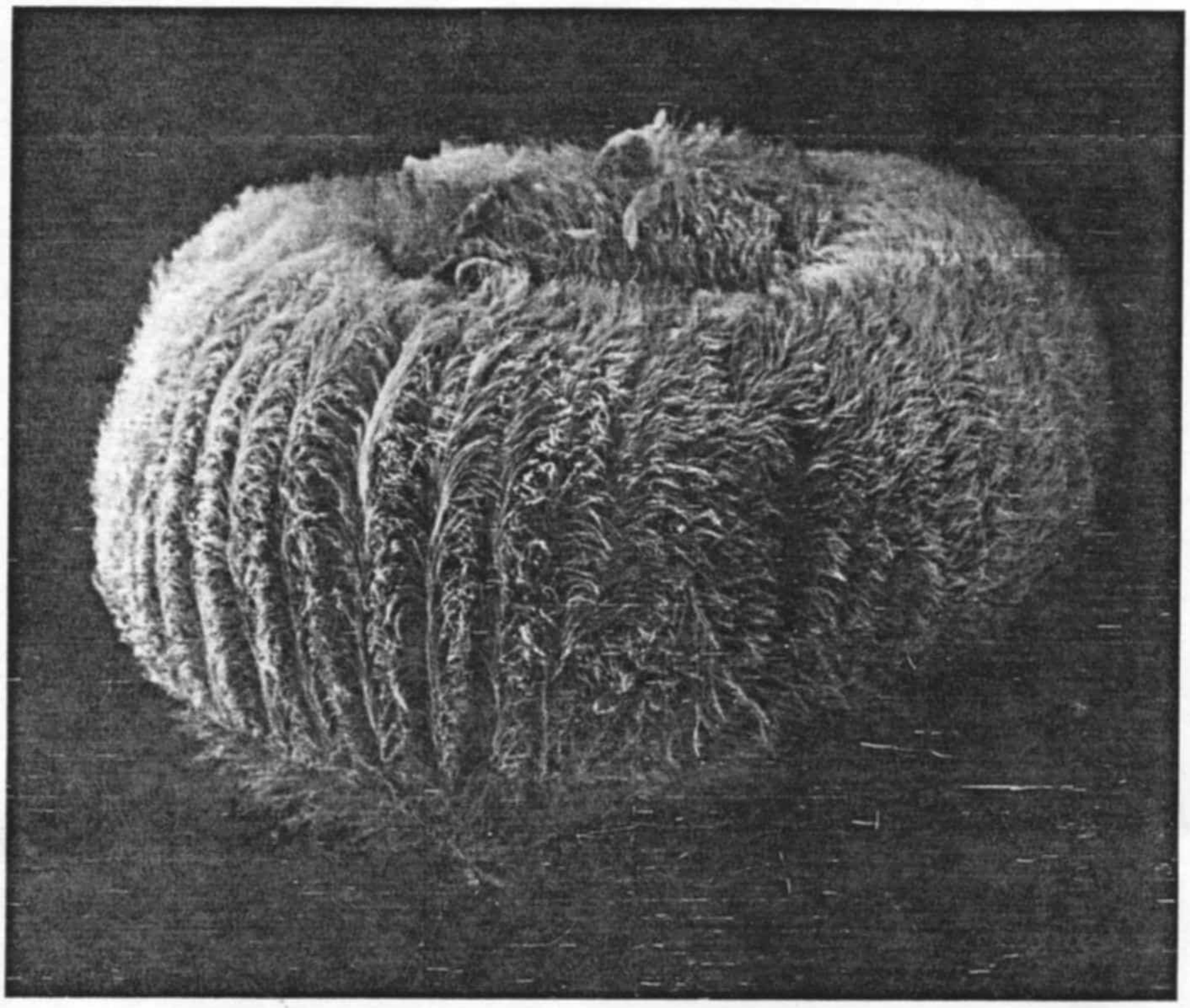


of sharp teeth called the radula. Once through the frontal membrane, the sea slug sucks out the polypide. What possible defenses might a bryozoan employ when confronted with such a terror? Some recent observations reveal that they don't just sit still.

One bryozoan, *Membranipora,* a species that incrusts brown algae and that is found all along the eastern edge of the Pacific Ocean, has been divided into species based on the patterns of spines on the zooids. In 1982, Paul Yoshioka, a biologist at the Scripps Institution of Oceanography, noticed that spiny colonies of *Membranipora* only occurred when nudibranchs were found in association with them. He therefore made the intriguing proposal that the various spine patterns reflected, not different species, but an individual colony's response to grazing by sea slugs. According to Yoshioka, the spines are physical defenses against the depredations of nudibranchs; like the tannins in sugar maple leaves, the *Membranipora* spines make the colony less attractive to foragers. Next, Drew Harvell,

Scanning electron microscopy reveals spines on two Pacific species of bryozoan: Callopora craticula, *top left, and* Membranipora angulata, *bottom left. Spines may grow in response to predators or other environmental factors. Below: The larva of the bryozoan* Dendrobeania lichenoides.

Christopher G. Reed



now on the faculty of Cornell University, followed Yoshioka's lead and demonstrated that colonies of *M. membranacea* were capable of forming spines within forty-eight hours of exposure to the nudibranchs.

Because of these discoveries of "inducible" defenses, the rich bryozoan fossil record, which only preserves the calcified skeletal parts of colonies, should be interpreted with caution. Rather than indicating separate species, the spine patterns may only reveal how much predation a particular colony had experienced back in the Mesozoic era. The ecological features of long-extinct communities, features that we have believed to be unknowable, may be recorded in the skeletal shapes of bryozoans.

Perhaps the greatest struggle for a bryozoan is finding enough space in which to live and grow. Plankton provides a virtually boundless source of nutrition, but bare space—whether on a rock or on the surface of an annual alga—is only fleetingly available in the marine world. Bryozoans vary in how well they compete for space. Within a single community on the underside of a rock or coral head, there may be a hierarchy in which one species overgrows another species, which is overgrowing yet a third variety. A colony of a single species may occupy space only ephemerally, growing out at the margins by the asexual replication of zooids in a radiating fashion, like a fairy ring of mushrooms or a ring of ferns, until it is overtaken by a superior competitor.

If you could speed up time, you would find the boundaries of your orchard constantly changing. You would see it growing around and even over orchards with different species of trees, or perhaps being overgrown in turn. When you look at the mosaic of different colonies of bryozoans on the underside of a rock in the intertidal zone, what you are really seeing is a silent, life-or-death struggle for space. And as in all warfare, the combatants may use any advantageous technique to remain alive. Some bryozoans grow spines not only to retard predators but also in response to superior competitors; the spines apparently enhance their ability to resist overgrowth. Others are readily overgrown from behind but are able to resist overgrowth if they meet the competitor at their growing margin. Some species even seem to be able to change their direction of growth when encroached upon by a superior competitor. Such observations raise questions; for example, how does the colony sense the presence of a "superior" species before contact has occurred?

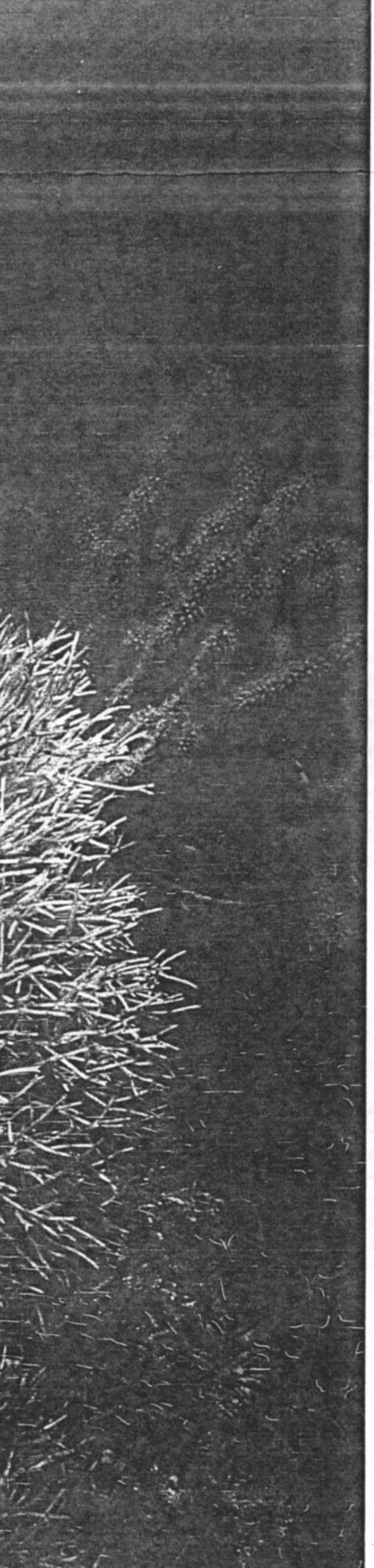
Colonies of the same species are equal competitors but inhibit one another's growth by contact. In *M. membranacea,* each colony may send out a quick-growing, specialized zooid that forms a stolon—a stemlike, cylindrical structure—along the margin of the encroaching colony. The stolon inhibits the further growth of the competing colony, and the space on the near side of the stolon is essentially reserved for expansion of the colony that sent it out.

Other species may even form alliances with different kinds of animals. The incrusting bryozoans *Celleporaria brunnea* and *Schizoporella errata,* for example, have a symbiotic relationship with a small colonial hydroid, *Zanclea gemmosa,* that grows over the surface of the bryozoan colony and along its growing margins. The hydroid apparently receives increased protection from grazers because its own, rootlike stolons are covered by the calcification of the bryozoan, while the bryozoan benefits from the presence of the hydroid's stinging cells on polyps around the margin of the colony.

Schizoporella also protects itself with regularly spaced jawed zooids, called avicularia, that snap shut at the slightest vibration. These specialized members of the colony undoubtedly reduce the likelihood of the surface's becoming colonized by algae and larval invertebrates, although the symbiotic hydroid seems not to be deterred.

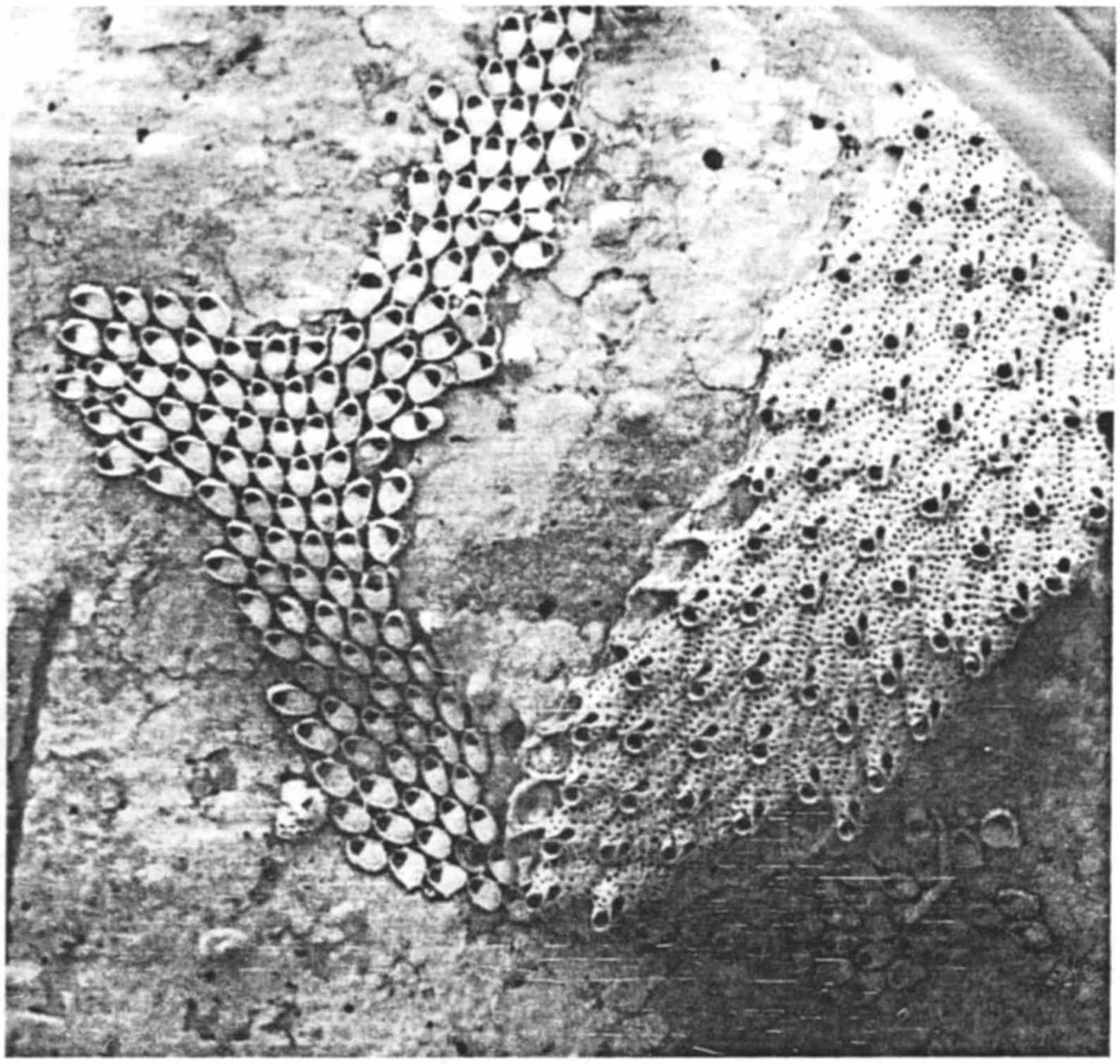
Once a colony of bryozoans is bounded by other colonies and can no longer spread by cloning itself, it shifts its energy into sexual reproduction. Clumps of writhing spermatozoa are released through the tips of the tentacles to be carried by water currents over other colonies of the same species, where they are drawn down into

Norbert Wu



A large bryozoan colony, left, blankets a rock in the Sea of Cortés, Baja California. Below: Two Caribbean bryozoans compete on a piece of Jamaican coral: Reptadeonella, *growing from right to left, is overtaking a colony of* Mollia. *Both species grow on the undersides of corals and in the caves of coral reefs.*

Barbara P. Worcester; AMNH



the feeding current of the zooids. But instead of being eaten, the spermatozoa attach themselves to the tentacles of the polypide. When an egg appears in a short, ciliated funnel at the base of the tentacles, the spermatozoa disengage themselves and swim down to the funnel, where fertilization is presumed to occur.

The situation just described occurs only in free-spawning species, of which *Membranipora* is an example. Most bryozoans, however, retain their eggs in elaborate helmet-shaped brood chambers, called ovicells, on the colony surface. In an "orchard" of *Schizoporella,* the brood chambers are specialized zooids, resembling geodetic domes, that erupt between the "trees." In each translucent, partly calcified ovicell is a heavily yoked, reddish embryo.

The larva that emerges from the ovicell following the embryonic period is a cilia-covered sphere ranging from .1 to .5 millimeter in diameter. It may be best visualized as an orange dipped in honey and then rolled on a barbershop floor; the rows of hairs (the cilia) all beat in synchrony, propelling the orange through the water. This highly organized, discriminating organism with its complex nervous system responds to light and gravity and exhibits specific preferences. The larva is choosy about where it will settle and what it will settle on to become the progenitor of the adult colony. Evolutionarily, this is a prudent adaptation, since the neighborhood a bryozoan finds itself in may determine the size and fecundity of the colony. Once the larva settles, it cannot pack up and move if the neighborhood goes bad. Some larvae can defer settling down in the presence of a superior spatial competitor, thereby reducing the likelihood of overgrowth early in the development of the colony. And some larvae settle only on a specific substrate, such as the blades of brown algae. These apparently maximize their potential growth as adults by settling preferen-

Besides being overgrown by competitors, bryozoans face being destroyed by the depredations of shell-less snails known as nudibranchs. Here, a Pacific coast nudibranch, purple aeolis, grazes on a colony of lacy crust bryozoans incrusted on kelp.
Susan Speck

tially on the youngest areas of the blades.

In our *Membranipora* orchard, the fertilized eggs, or zygotes, are initially shaped like biconcave disks. Spewed out into the seawater like so many Frisbees, the zygotes sail away to develop into peculiar triangular bivalved planktotrophic larvae. Known as cyphonautes, or little sailors, these beautiful, transparent larvae were initially thought to be rotifers, planktonic animals with a wheel of cilia, probably because they bear no resemblance to the benthic adult colony that they eventually become.

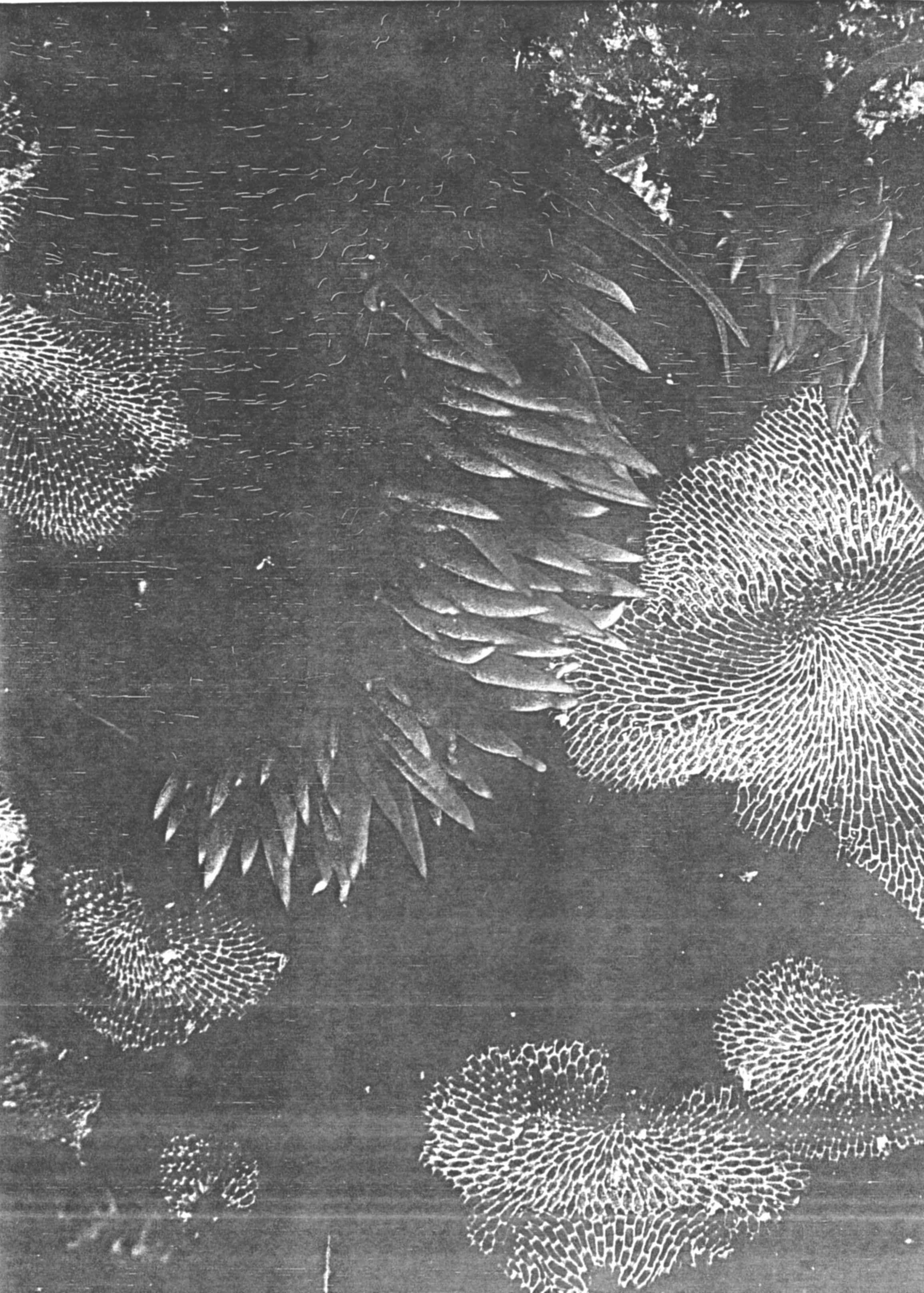
Metamorphosis transforms the free-swimming larva into the sessile progenitor of the colony, called the ancestrula (the first zooid of the colony). The sense of wonder and mystery that this process holds for those who are fortunate enough to observe it is reflected in the words of Thomas Hincks, a prominent nineteenth-century bryozoologist:

> The larvae are restless in their habits, and during their short term of free existence are in almost constant movement, now whirling rapidly hither and thither, now tumbling over and over in the water, now creeping along, making use of their cilia as feet. Besides their ciliary appendages, they are often furnished with long setiform processes, which wave to and fro, and lash the water with much vehemence. After a while their energies fail, and they settle down and become attached; the cilia begin to flag in their movements, and soon disappear; and the volatile and curiously organized being resolves itself into a fixed and (apparently) homogeneous mass, in which the first zooecium and polypide originate.

Hincks's description illustrates the sharp contrast between the motile, vibrant, free-swimming larva and the sessile, apparently quiescent juvenile. The rapid transformation and massive degeneration of larval tissues led most early investigators to view bryozoan metamorphosis as a completely destructive process. The adult organs were thought to develop *de novo* from this amorphous mass.

But this is not the case. Bryozoan larvae have organs specifically adapted for swimming through seawater, selecting an appropriate substrate, and attaching. They are equipped with larval locomotory and sensory organs consisting of ciliated regions of the larval epithelium. The adult epidermis, or skin, is tucked away in invaginations, dormant, awaiting the moment when it will be needed. This moment is metamorphosis. At the onset of metamorphosis, the larva absorbs its larval skin and covers itself with the adult skin by a series of rapid movements that essentially turn it inside out within minutes. At the same time, the adult skin begins secreting the protective calcified exoskeleton (the zooecium). The digestive tract of the first polypide also begins to differentiate, drawing nutrition from the degeneration of the yolk-laden larval tissues. Far from being a period of quiescence, this is a time when adult structures are developing and differentiating while unneeded larval tissues degenerate. Suddenly a mobilization of phagocytes—scavenging cells—engulfs and digests the larval tissues. These simultaneous processes of cell death and cell rejuvenation, side by side in the same organism, remain a fundamental mystery to developmental biologists. How do the phagocytes distinguish between cells destined to die and those destined to live? What controls the clock that synchronizes these processes into the recurrent patterns of metamorphosis that we observe in so many different species? A plethora of mysteries remains to be explored in this little-known phylum.

The turbulent world of bryozoans is a shady, shadowy twilight world—undersides of rocks or floats where competition with marine plant life is minimal. Suddenly, as the twilight is shattered by brilliant sunlight, the lophophores struggle in vain to extend themselves to extract food from the life-giving seawater. But the medium has changed, and the lophophores are now exposed to the air. The temperature slowly rises, baking the exposed zooids and leaving the dry and lifeless skeleton of the colony bleaching in the midday sun. Strolling farther down the beach, the person responsible for these new conditions leaves other rocks overturned, unaware or perhaps unmindful of the catastrophic consequences to the microcosmos beneath. □



Fascinated by the "abrupt, often cataclysmic metamorphoses of marine sessile invertebrates," marine biologist **Christopher G. Reed** (page 40) specialized in the morphology and development of bryozoans, brachiopods, and polychaetes. Reed grew up on Vashon Island, in Puget Sound near Seattle, and developed an early, ardent interest in natural history. He was educated in his native state, earning both bachelor's and doctoral degrees in zoology from the University of Washington and doing fieldwork at the university's Friday Harbor Laboratories in the San Juan archipelago. In 1980 he came east for a postdoctoral fellowship at Harvard, and in 1982 he joined the Department of Biology at Dartmouth College in Hanover, New Hampshire. Known as a witty and enthusiastic lecturer who inspired students, at Dartmouth Reed twice received special recognition for distinguished teaching. Although bryozoans were his first love, Reed also enjoyed studying vertebrates and made many observations of skunks, raccoons, snakes, owls, and bats in the wild. After an extended illness, Christopher Reed died in January 1990 at the age of 38. He left a wife and an infant daughter. The Christopher Reed Memorial Fund, which assists student research at the Friday Harbor Laboratories, has been established at the University of Washington Office of Gift Policy, Seattle WA 98195.